INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

LAGOA DA PATA REVISITADA: MAIOR SAZONALIDADE COMO CAUSA DO REAGRUPAMENTO DA COMUNIDADE VEGETAL DURANTE O ÚLTIMO PERÍODO GLACIAL NA AMAZÔNIA

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Mestre em CIÊNCIAS BIOLÓGICAS, área de concentração em BOTÂNICA.

MANAUS-AMAZONAS
Março, 2010

D212 D'Apolito Júnior, Carlos
Lagoa da Pata revisitada: maior sazonalidade como causa do reagrupamento da comunidade vegetal durante o último período glacial na Amazônia / Carlos D'Ápolito Júnior.--- Manaus : [s.n.], 2010.
53 f. : il.

Dissertação (mestrado)-- INPA, Manaus, 2010
Orientador : Maria Lúcia Absy
Área de concentração : Biodiversidade Vegetal da Amazônia, Reprodução e Crescimento de Vegetais

1. Paleopalinologia. 2. Paleobotânica. 3. Amazônia – Período glacial .
I. Lagoa da Pata revisitada: maior sazonalidade como causa do reagrupamento da comunidade vegetal durante o último período glacial na Amazônia.

CDD 19. ed. 561.13

Agradecimentos

Ao Programa de Pós-Graduação em Botânica do Instituto Nacional de Pesquisas da Amazônia.

Ao Conselho Nacional de desenvolvimento Científico e Tecnológico (CNPq), pela bolsa de mestrado e auxilio financeiro.

À Dra. Maria Lúcia Absy, minha orientadora, por me receber e me proporcionar um grande início na linha de pesquisa que escolhi.

À Coordenação de Pesquisas em Botânica (CPBO) - Dra. Maria das Graças Vieira.

Ao Dr. Edgardo Latrubesse, pela idéia do projeto e ótimas dicas.

A Dra. Elena Franzinelli pela incansável ajuda, disposição, atenção e compromisso conosco.

Aos docentes do Programa de Pós-Graduação e Botânica e outros pelos ensinamentos.

À minha família por todo apoio e por acreditar em mim.

A todos os colegas do curso, com quem fiz ótimos cursos e compartilhei bons momentos de estresse e alegria.

Aos Companheiros de república (André, Carol, Letícia, Mariana, Pedrinho e Téo), sem eles a vida em Manaus teria sido certamente mais difícil.

Aos colegas do laboratório de palinologia, Cleonice, Caroline, Isabella, Marquinhos, Otilene, André e Natália, Sabrina, Jéssica, Hugo, Wittor e Gabriel.

Ao colega Mário T. Araújo e seus companheiros de trabalho em campo no Morro dos Seis Lagos, que me possibilitaram a obtenção de algumas amostras de pólen das suas coletas botânicas.

Aos avaliadores do plano de dissertação, Drs. Hailton Igreja, Florian K. Wittmann, A.Carlos Webber, Elena Franzinelli e Márcia A. de Barros, e em especial a Dra. Caroline Scherer que me elucidou diversas questões metodológicas.

E por fim, mas não por menos, ao meu corpo por ter permanecido “saudável” mesmo com momentos de muito estresse.

Epígrafe

"*A igualdade nos faz repousar.*
A contradição é que nos torna produtivo."
Johann Wolfgang Von Goethe

Resumo

Pólen em sedimentos da Lagoa da Pata, noroeste da Amazônia, foi estudado com o intuito de cobrir o último ciclo glacial. Embora uma floresta tropical alta pareça ter remanescido intocada durante os últimos ~120,000 anos, a re-análise e reinterpretação de dados sugerem que a vegetação não análoga da idade do gelo na Amazônia foi mais sazonal, assemelhando-se às florestas tropicas sazonalmente secas. O resfriamento teve papel importante em permitir a expansão local de elementos montanos, que é o ponto chave para estabelecer uma vegetação sem análogos modernos. A interpretação paleoambiental estritamente local não pode ser extendida a uma região mais ampla da planície, pois, como presentemente, chuvas orográficas fizeram com que o morro onde o lago está localizado permanecesse mais úmido e menos suscetível a seca, ao contrário das florestas na planície da alta bacia do rio Negro. Seco e moderadamente mais frio é o mais provável cenário climático para a região durante picos do último glacial.

Abstract

Pollen in sediments of Lake Pata, northwestern Amazon, was studied with the aim of covering the entire last glacial cycle. Although a tall tropical forest seems to have remained unbroken throughout the past ~120,000 years, reanalyses and reinterpretation of data suggest the so-called nonanalog ice age vegetation was more seasonal, resembling present day seasonal tropical dry forests. This agrees with a prolonged annual dry season and polar air advection as the features setting the region biome. The very local paleoenvironmental interpretation cannot be perfectly extended to a broader lowland region because like presently, orographic rain caused the hill to have remained moister and less susceptible to drought, unlike the overall mesic lowland forests of the upper Rio Negro basin. Thus the dry events affected the region more drastically than what could have been assessed by means of a pollen study at the hill. Seasonally dry and moderately cooler is the most probable climatic picture for the region during the last ice age.

Sumário

Introdução

Nas últimas décadas, um grande corpo de literatura tem sido devotado a explicar paleoambientes na bacia amazônica. Tradicionalmente a palinologia traz grandes vantagens nos estudos paleoecológicos, mas a incorporação de diferentes métodos tem culminado em registros mais detalhados e acurados que se tornam proxies convergindo de várias áreas do conhecimento. Entre os locais de estudo palinológico na Amazonia, o Morro dos Seis Lagos é um bom exemplo disto. Ao diagrama original (Colinvaux *et al*, 1996), análises paleoquimicas foram adicionadas (Bush *et al*, 2002), que permitiram aos autores inferirem as causas dos ciclos orbitais nos regimes de precipitação locais. Esses autores, acima citados, combinaram pesquisas palinológicas com estudos geoquímicos cujos resultados possibilitaram detalhar uma história ambiental para as condições do glacial tardio na Amazônia. (Bush *et al,* 2004).

A lagoa da Pata é um dos poucos pontos da Amazônia que preservou uma história contínua, ou quase contínua. Uma lacuna na sedimentação é clara entre 35 e 26 mil anos antes do presente, embora mudanças na vegetação não tenham sido detectadas, e a fase mais seca parece então ter ocorrido neste período ao invés do último máximo glacial (UMG). Entretando, a sedimentação em 18 mil anos atrás é questionável pelo fato de que argilas nodulares talvez indiquem retrabalhamento (Ledru *et al*, 1998), e até mesmo um evento seco durante o Holoceno inicial a médio é evidente pela sedimentação e conteúdo polínico (Mayle and Power, 2008). Não obstante a existência de um hiato sedimentar (Ledru *et al,* 1998; Van Der Hammen and Hooghiemstra, 2000) ou pelo menos um forte decréscimo na precipitação (Hooghiemstra and Van Der Hammen, 1998), a lagoa da Pata é constantemente citada como um registro de floresta intocada, tanto por aqueles que advogam a favor de uma vegetação fragmentada durante o último máximo glacial -UMG- (Hooghiemstra and Van Der Hammen, 1998; Van Der Hammen and Hooghiemstra, 2000; Haffer and Prance, 2002) ou pelos que se opõem a ela (Colinvaux and De Oliveira, 2000, 2001; Colinvaux *et al*, 2001). Os mapas de cobertura da vegetação durante o UMG até hoje publicados (Van Der Hamenn and Absy, 1994; Bush, 1994; Haberle and Masli, 1999; Hooghiemstra and Van Der Hammen, 1998; Anhuf *et al*, 2006) geralmente colocam a lagoa da Pata no limite de um grande bloco de floresta pluvial a oeste, cercado por vegetação tipo savana ou semidecídua. A manutenção de floresta pluvio-tropical parece improvável, assim como a extrema expansão de savanas, o que tem levado a reconstruções mais mosaicas

(Cowling *et al*, 2001; Anhuf *et al.*, 2006), embora diferentes interpretações, principalmente pelo falta de dados, ainda sejam possíveis (Anhuf *et al*, 2006).

O núcleo de sondagem retirado da lagoa da Pata tem quase sete metros de profundidade e passa dos 170 mil anos, que foi inferido por uma interpretação peleoquimica de cátions de potássio bem correlacionados com ciclos precessionais (Bush *et al*, 2002), sendo assim usados para extrapolação da datação basal. Constringindo a idade basal do núcleo em 170 mil anos por meio do uso da natureza cíclica dos picos de potássio (oito ao total) assume uma taxa de sedimentação constante, que por sua vez está de acordo com uma simples extrapolação das datações radiocarbônicas dos 1,5 metros superiores, considerando uma sedimentação constante. Apesar de que o núcleo completo possa compreender dois ciclos glaciais completos, iniciando no estágio isotópico 6 (MIS6), dados de pólen foram publicados apenas para os últimos 50 mil anos.

Objetivos

Geral

Analisar pólen contido em amostras de sedimentos, cobrindo um ciclo glacial inteiro, portanto atingindo MIS 5e bem como averiguar a evolução da paisagem no Morro dos Seis Lagos durantes os últimos 120 mil anos.

Específicos

Testar a replicabilidade dos dados, uma vez que boa parte do estudo já foi realizada por outros pesquisadores.

Comparar metodologias usadas antes e no presente estudo.

Verificar se conjuntos de dados de outras naturezas se assemelham ou não aos aqui produzidos.

Lake Pata revisited: increased seasonality as a cause of community reassortment in the ice age Amazon vegetation

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Abstract

Pollen in sediments of Lake Pata, northwestern Amazon, was studied with the aim of covering the entire last glacial cycle. Although a tall tropical forest seems to have remained unbroken throughout the past ~120,000 years, reanalyses and reinterpretation of data suggest the so-called nonanalog ice age vegetation was more seasonal, resembling present day seasonal tropical dry forests. This agrees with a prolonged annual dry season and polar air advection as the features setting the region biome. The very local paleoenvironmental interpretation cannot be perfectly extended to a broader lowland region because like presently, orographic rain caused the hill to have remained moister and less susceptible to drought, unlike the overall mesic lowland forests of the upper Rio Negro basin. Thus the dry events affected the region more drastically than what could have been assessed by means of a pollen study at the hill. Seasonally dry and moderately cooler is the most probable climatic picture for the region during the last ice age.

Key words: fossil pollen, Amazon, glacial, seasonal.

1. Introduction

Over the past few decades a large body of literature has been devoted to explain paleo-environments in the Amazon basin. Traditionally, palynology fairly contributes to paleoecological studies, but the incorporation of different methods, proxies converging from various research areas, has led to more accurate and detailed records. Among the pollen sites in the Amazon, the Hill of Six Lakes is a good example of such picture. To the original diagram (Colinvaux *et al*, 1996) paleochemical analyses were added (Bush *et al*, 2002), which allowed the authors to infer the causes of orbital forcing on local precipitation regimes.

Lake Pata is one of the few pollen sites in the Amazon that preserved a continuous, or almost continuous, history. A gap in sedimentation is suggested between 35,000 and 26,000 years before present, and the driest phase seems therefore to have occurred in this period rather than in the last glacial maximum (LGM). Nevertheless, the sedimentation at 18,000 is questionable due to the fact that nodular clays may indicate sediment reworking (Ledru *et al*, 1998), and even a pronounced dry early-mid Holocene event is evident from both sedimentation rate and pollen (Mayle & Power, 2008). Regardless of the existence of a sedimentary hiatus (Ledru *et al*, 1998; Van Der Hammen & Hooghiemstra, 2000) or at least a markedly lower estimated precipitation

(Hooghiemstra & Van Der Hammen, 1998), Lake Pata is constantly cited as a record of unbroken forest, either by those who advocate in favor of a more fragmented LGM Amazon vegetation (Hooghiemstra & Van Der Hammen, 1998; Van Der Hammen & Hooghiemstra, 2000; Haffer & Prance, 2002) or those whose interpretations oppose it (Colinvaux & De Oliveira, 2000, 2001; Colinvaux *et al,* 2001). The published maps of vegetation cover during the LGM (Van Der Hamenn & Absy, 1994; Bush, 1994; Hooghiemstra & Van Der Hammen, 1998; Haberle & Masli, 1999; Thomas, 2000; Anhuf *et al*, 2006) generally place the area of Lake Pata on the edge of a major evergreen forest block westwards, which is surrounded by savannah-like or semideciduous vegetation. Both views support the fact that the maintenance of untouched evergreen forest in Amazonia during glacial times seems unlikely and so does an extreme savannah expansion, which has led to more mosaic reconstructions (Cowling *et al,* 2001; Anhuf *et al.*, 2006), though different interpretations, due mainly to limited data, are still possible (Anhuf *et al,* 2006).

The core raised from Pata is almost seven meters deep and spans the last 170,000 years, which was inferred from a palaeochemical interpretation of K^+ cation peaks well correlating with precessional cycles (Bush *et al,* 2002), thus being suitable for an age extrapolation. Constraining the basal age of the core in 170,000 by means of using the cyclic nature of the potassium peaks (eight) leads to the assumption of a constant sedimentation rate throughout the complete core, which in turn is in agreement with a simple extrapolation of ^{14}C dates from the upper 1,5 meters. Despite the whole core is suggested to comprises two complete glacial cycles, beginning at the marine isotope stage 6 (MIS 6), pollen data were published for the last 50,000 years only. The objective of the present study is to analyse pollen in sediments covering one full glacial cycle, hence reaching MIS 5e. As a matter of fact, the replicability of pollen analyses can be therefore tested since a large part of the core is being re-analysed, and methodological comparisons will be drawn so as future compilations and reviews take into consideration inherent analytic differences of pollen studies.

1.2. The Six Lakes Hill (Morro dos Seis Lagos)

The hill rose after a cretaceous magmatic intrusion (Schobbenhaus, 1984), which also created some other smaller rock outcrops near the Six Lakes, that is located at 0°16'N - 66°41'W. The site occupies the Rio Branco-Rio Negro Pediplain at an elevation of 300 meters (Viegas-Filho & Bonow, 1976). Climate is the typical equatorial warm one. The northwestern region of the Amazon basin does not experience a real dry season; there is no month when rainfall is less than 100 mm and annual rainfall ranges around 3000 mm (Sombroek, 2001). The main source of rain is a continental-equatorial air mass, product of ground/vegetation cover evaporation.

The little information on vegetation of the Six Lakes Hill comes from the previous study of Bush *et al* (2004), where field observations of the vegetal composition and physiognomy are commented; from RADAMBRASIL (1976), Projeto Seis Lagos held by CPRM (Viegas-Filho & Bonow, 1976), communications with some colleagues who performed botanical collections at the hill (M. T. Araújo and A. C. Weber) and checking some few herbarium sheets from Six Lakes collections (INPA Herbarium-Manaus). The edaphically-constrained vegetation is similar to those of white sand vegetations (heath forests; Whitmore, 1984), not only structurally but also taxonomically. Nevertheless, for the occurrence of true dense-forest trees, bare rock/very thin soil areas, open areas with typical secondary forest elements, the overall vegetation growing on the hill is better called a mixture rather than one single type. At some points, like the Esperança swamp and lakes surroundings, *Maurita*, *Mauritiella*, *Euterpe* and *Ludwigia* are recorded. RADAMBRASIL (1976) includes the Six Lakes Carbonatite into the dense forest classification and point out the high abundance of the tree macucu-de-paca (*Aldina latifolia* Spruce ex Benth.). Furthermore, other *taxa* reported as abundant are *Alchornea, Ouratea*, Melastomataceae, Clusiaceae and palms.

Modern pollen spectra obtained from moss polsters during one single field work shows high abundance of *Alchornea/Aparisthmiun* that though unusual is reflected in the percentages found in Holocene and Pleistocene sediments of lakes Pata and Verde (Bush *et al,* 2004). Other common forest elements were also identified, mostly trees, and very few herbs.

2. Methods

The sediments analysed in this survey come from one parallel core drilled by P. Colinvaux and his colleagues in October of 1991. The field procedure for coring is detailed in Colinvaux *et al* (1999) and more information is found in the methods of Bush *et al* (2004). In the occasion of their work in the Amazon, facilitations were provided by the Federal University of Amazonas (Manaus-AM), where one of the parallel cores was left as testimony material. This core was taken to Italy where Antonio Rossi performed mineralogical analyses at the Universitá delgi Studi di Modena (Modena-Italy). Later, subsamples were taken for pollen analyses at the National Institute for Amazon Research (INPA-Manaus-AM).

During one excursion held in the nineties by a group of INPA, a moss polster near Lake Pata had been collected as asked by one of us (MLA) and since then properly stored. This is now used for pollen rain.

Two centimeters subsamples were weighed (around 2 grams) at more or less 10 cm intervals. *Lycopodium clavatum* tablets (Batch n° 177745) were added for absolute counting (Stockmarr, 1971) and the methodology used was the standard one: 10% KOH, acetolysis and heavy liquid separation by bromoform (Faegri & Iversen, 1989). Residues were mounted in glycerin gelatin. Precisely 300 pollen grains were counted per sample and other palynomorphs (Pterydophyte spores, algae and fungal spores and hyphae) were counted in parallel to the 300 pollen sum. Pterydophyte spores were separated in every different morph and identified when possible, but algae and fungal spores and hyphae were not. The percentages of spores were based on the pollen sum plus spores sum, algae and fungal remains are presented in the percentage diagram as abundances. The concentration of algae within the sediments was remarkably high, thus it was counted 300 algal cysts per sample and the total abundance paralleling 300 pollen grains is estimated from a simple rule of three. Bush *et al* (2004) set a “rule of thumb” stating that small tricolporate pollen much likely come from trees and shrubs, so they included the unknown tricolporate pollen within the arboreal sum. Based on their evidences and experience on palynology the arguments given for this rule of thumb were that other ecologic groups are more easily identified, like herbs, montane taxa and taxa favored by disturbance but small tricolporate grains from the species rich forests are more complicated to divide into types. We generally agree with this statement as it seems quite reasonable. Nevertheless, unknown pollen grains will not be included within the arboreal sum here. What is more, the precise counting of 300 grains and the differentiation of palynomorphs into as many types as possible gives a more detailed impression to the pollen diagram and hence may diminish the subjectivity carried by different pollen analysts.

Pollen identification was aided by pollen illustrations and descriptions published by Absy (1975, 1979), Hooghiemstra (1984), Roubik & Moreno (1991) and Colinvaux *et al* (1999). The Amazon pollen manual and atlas (Colinvaux *et al*, 1999) contains photomicrographs and morphological descriptions of pollen and spores obtained from lake sediments from the Six Lakes Hill, thus being a major aid for identification here, on the one hand. One the other, after comparing the images within the atlas with pollen slides of the pollen collection at the Palynology Laboratory (INPA) we realized that some *taxa* were doubtful, even considering possible intraspecific variation. For instance, the pollen of *Citrus* is listed but this is an exotic species to South America, unless this pollen was found in very recent sediments or a transoceanic dispersion brought some *Citrus* pollen to the lake, it is misidentified (as we think it is). In addition, some *taxa* in the pollen diagram of Bush *et al* (2004) are not described and illustrated in Colinvaux *et al* (1999) and even Lecythidaceae that are present in the very original diagram (Colinavaux *et al,* 1996) were as well not included in the atlas. We think that if a *taxon* is present in a pollen diagram it occurs more than once in the fossil record (usually pollen diagrams include *taxa* more than 2%) and hence it is strange that the atlas of Colinvaux and his colleagues omits some *taxa.* This is quite evident when one realizes that the more refined pollen taxonomy presented in the diagrams of Bush *et al* (2004) contain *taxa* that are absent in the 1999 atlas. Palynology of neotropical plants is a hard taxonomic task yet in need of intense study, and we are well aware of the expected divergence among different palynologysts, although we found some pollen identifications to be a bit doubtful it is not our aim to discredit the Amazon pollen manual and atlas of Colinvaux *et al* (1999) which still is one of the few guides for amazon pollen taxonomy.

The main identification reference used was the pollen collection of the Palynology Laboratory and recent botanical collections at the Hill of Six Lakes performed by a group of INPA added new species that could be compared with the fossil types. Pollen diagrams were built using the program TILIA and TILIAGRAPH

(Grimm, 1992) and the separation of pollen zones aided by CONISS (Grimm, 1987). Percentage diagrams present *taxa* ≥ 1%, the rest is grouped within life form or family diagrams. Concentration diagrams present *taxa* ≥ 5.000 pollen per gram. The hollow curves within the diagrams are six times exaggerations.

The stratigraphy of the parallel core analysed here is the same as the cores previously studied (as described in Bush *et al*, 2004). The chronology was established based upon carbon dates of a principal and a parallel core. ^{14}C dates used for a compared chronology come from three cores already published (two cores in Bush *et al*, 2002, 2004 and one core in Santos *et al*, 2001), where all dates are presented in detail. Dates in the pollen diagrams are the same ones as in Bush *et al* (2004). More general information is given in Barbosa *et al* (2004), with new dates from two different cores.

3. Results

3.1. Core Stratigraphy and Chronology

The core is composed of 200 cm carbon rich sediments (regarded as black gyttja) with a discontinuous unity between 60–83 cm which has evidences of oxidation (regarded as nodular yellowish clay). Indeed, 60-63 cm is a thin transitional layer that resembles the oxidized lower unity. The upper 60 cm are pure black gyttja, similar to the gyttja from 83-200 cm, but softer. From 200-300 the composition of the sediments is a brown silty clay, and at two levels (around 205 and 305 cm) this silty clay is of a darker brown.

In order to establish a good chronology (Fig. 2), 15 carbon dates were used from the original coring (Bush *et al*, 2002, 2004), and 15 from a different core published by Santos *et al* (2001). The dates in the first two cores provide a robust chronology, but a possibly problematic point, not mentioned before, was found: two dates of 35 BP Ky (ages will be expressed as kilo years Before Present; Ky BP) were obtained at different levels of the principal and parallel core, 105-110 cm and 84.5 cm, respectively. The date at 84.5 was adopted as it is continuous to another one at 82 of the same core and both comprise a smaller interval of sediments.

Sedimentation during the upper Holocene (from ~6 Ky BP onwards) and early-mid glacial (>45-35 Ky BP) are similar, ranging around 0.01 cm year^{-1}. The period comprised between these phases demonstrates lower rates of deposition (0.001 and 0.0002 cm year^{-1}) and pollen concentration (around 48,000 grains/g). Data of Santos *et al* (2001) show a general similar trend in sediment accumulation but a very discrepant point is noticed, an erosional event during the last glacial maximum (arrow in Fig.2), evidenced from the noludar clay unity consistent with a high depositional rate from reworked sediment rather than extremely low sedimentation rate as explained by Colinvaux *et al* (2000) and Bush *et al* (2004). Although published prior to the new pollen work, Santos *et al* (2001) is not cited by Bush *et al* (2004).

The cores studied by Santos *et al* (2001) and Barbosa *et al* (2004) were analysed regarding total organic carbon (TOC) and water content. What corresponds to the erosional unity (~30 to 15 Ky BP), much lower carbon was recorded, water is also lower but the lowest water level content is actually found around 15-10 Ky BP. The authors explain this hiatus as a result of torrential rains in a more seasonal and cooler climate, which made sediments to be remobilised with the deposition of clastic material.

3.2. Pollen rain—por as zonas aqui....pollen rain antes…

The sample of moss polster analysed for pollen rain yielded a richness of 41 *taxa* of pollen and only two types of pterydophyte spores (Fig. 3). Such richness is higher than the average of five other samples analysed by Bush *et al* (2004), that was 32.2, but the spectra identified is similar. The most striking difference was an extreme dominance of *Protium*, only explained by trees of this genus being near the moss polster when collected, not to mention that moss polsters as pollen rain indicators fail to comprise longer periods of the year, but generally few months. *Alchornea/Aparisthmium* are important but not as abundant as the previous analyses, contrarily to the statement that field observations did not match with this *taxon* being a major contributor to pollen rain (Bush *et al*, 2004), the recent botanical collections at the hill confirm *Alchornea/Aparisthmium* is very abundant, and thus a good tool to infer present day vegetation.

Much interestingly, we found two grains of *Myrsine*, like Bush *et al* (2004), who found one. This confirms that *Myrsine* may be presently contributing to the pollen spectra, or it might be that a related *taxon* misled us all to a wrong identification, in spite of *Myrsine* pollen being quite easy to identify.

Many *Anthurium* pollen and another probably Araceae pollen were found, their non representation in the fossil spectra is much probably due to selective preservation as these grains are fragile. Moraceae/Urticaceae is relatively abundant (10%), in the previous study it reached 15% in one sample, out of five, but is generally less frequent. In relation to spores, 25 monoletes were counted and only one *Selaginella*, making up 12% of the pollen sum.

3.3. Pollen taxonomy and ecological features

The overall taxonomic resolution was very similar to the previous published identified *taxa*. However, some differences are evident and will be concerned here. Firstly, pollen types of *Mauritia* and *Mauritiella* were thought to be distinguishable and thus compose two different diagrams. Indeed, some morphological variation may rise uncertainty in distinguishing them, but two morphotypes (Fig. 4 a-b) were so clear that any error in separating them is smaller than gathering them into one single type. The most evident difference, which actually made us separate them, was observed in one sample (55-57 cm) where a high abundance of the *Mauritia* type was found. These two types were identified and separated in Colinvaux *et al.* (1999).

An important type, mainly in Holocene sediments, was safely identified as *Ouratea* (Fig.4 i-j and m-n) by comparing the fossil with an *Ouratea* recently collected at the hill (Fig.4 k-l and o-p), which is an abundant component of the mesic forest. This type is correspondent to *Copaifera* in the previous diagrams and atlas (Colinvaux *et al*, 1999, page 274, figure 219).

An abundant pollen grain through the entire core was identified as *Aldina* (Fig.4 g-h). It is possible that this type was previously misidentified as *Amburana aff. cearensis* (Colinvaux *et al*, 1999, page 277, figure 239), which is a typical genus occurring in the Cerrado and Caatinga vegetations. This fossil type was extremely similar to two *Aldina* species within our pollen collection (Fig.4 c-f), but we did not have the specimen presently occurring at the hill, which is locally very abundant (RADAMBRASIL, 1976 and M. T. Araújo, *personnal communication*) and thus ensures our identification. RADAMBRASIL (1976) lists “macucu-de-paca” (*Aldina latifolia* Spruce ex Benth) at the hill and at least four more vernacular names are cited to occur in the vicinities of São Gabriel da Cachoeira (Manaus-AM), for the fact that vernacular names are often unreliable at the species level (Ter Steege *et al*, 2006) we can be neither sure of the species level identification nor whether only one *Aldina* species occur at the hill. In addition, there are well documented varieties that probably contribute to pollen morphology variation. RADAMBRASIL’s phytogeographical inventories found *Aldina* broadly spread in the upper Rio Negro basin, occupying lowland and submontane dense tropical forests, open submontane forests with palms and dense alluvial or submontane arboreal Campinaranas (dense heath forests).

Some legume pollen grains are difficult to distinguish into reliable types and are generally grouped as Fabaceae (or its subfamilies), in the Pata fossil record some genera of the Caesalpinioideae and Papilionoideae prevented us from creating a subfamily group. Remarkably, *Bowdichia* and *Cassia* can be confused depending on the view, which many times is neither polar nor equatorial, but somewhat oblique. Apart from the types shown in Colinvaux *et al* (1999; figure 214, page 273 and figure 240, page 277) at least two other types of *Bowdichia* and *Cassia* in our pollen collection were seen to be hardly distinguishable.

Other taxonomic differences are minor and less important, other aspects of the present fossil record would be more relevant for a different paleoecologial interpretation than the pollen taxonomy itself.

Ecological affiliation groups were conservative, especially concerning the montane group. We have seen in overall literature, from herbarium sheets and communications with experienced colleagues that *Ilex, Humiria* and Ericaceae are commonly found in heath forests, not to mention that the present day pollen spectra at the hill shows *Ilex* relatively well represented, as well as Ericaceae. The genus *Gaylussacia* cannot be distinguished from *Agarista* (Colinvaux *et al*, 1999) and thus it is questionable whether the fossil type indicates cold conditions inferred from the *taxa* confined to montane vegetations, or arid conditions inferred from the present day distribution of shrubby *taxa* from Cerrados where both genera are recorded (Von Linsingen *et al*, 2006). Importantly, an indicator species of Campinaranas is *Gaylussacia amazonica* Huber, and hence its representation may indicate canopy openness. What is more, *Satyria panurensis* (Benth. ex Meisn.) Hook. f. ex Nied. That was collected has a very similar pollen to *Gaylussacia/Agarista*. For the above cited reasons we regard as montane taxa only *Podocarpus*, *Myrsine*, *Hedyosmum*, *Weinmannia* and *Alnus*.

3.4. Zoning

The pollen record of Lake Pata does not show too discrepant zones. The Holocene, the late glacial and the last interglacial are quite clearer than other zones, though strong biome changes are not intense. For both crude zones and sub-zones creation we used percentage and concentration data from pollen, spores, algae and fungal remains. The nature of sediments was also an important aspect taken into consideration for zonation, and so was dating, but dissecting the glacial into its phases did not influence pollen zones as much as the palynologycal assemblage itself. The CONISS dendrogram helped the zones setting but the main establishment was visual. The following descriptions reveal the main reasons why each zone was adopted according to palynological configurations that may be indicative or distinctively recognizable, at least at a local extant. Percentage diagrams are found in Fig. 5.

3.4.1. *Zone 1 (305-285 cm).* At the beginning of the record a high and distinctive peak of *Mauritia,* coupled with the nearly absence of monate elements (0-1,2%) and the indicative representation of palms, Ancardiaceae, Moraceae/Urticaceae, *Ouratea, Laetia*, *Casearia, Protium* and *Cecropia,* raise a great similarity with holocenic sediments. Concentration data (average of ~540,000 grains/g) are comparable to those of the Holocene, the same behavior is also found in the counts of fungal remains and algae. This zone is unique in a high occurrence of *Pteris/Pityrograma.*

3.4.2. *Zone 2 (285-200 cm).* This zone is subdivided into three periods, the first of which (2-A) has a peak in *Alchornea/Aparisthmium,* followed by slight increases in

Sagittaria, Anacardiaceae and *Protium,* a decrease in total ferns, and a still high concentration of algae and fungal remains. Total concentration (average of 165,000 grains/g) and the absence of *Mauritia* were indications for setting a new zone rather than extending zone 1 until the upper limit of sub-zone 2-A (247 cm).

Subsequently, 2-B has contrasting abundances of fungal remains and algae, though both concentrations are very low. Some important *taxa* have a markedly similar behavior in this zone (*Alchornea/Aparisthmium,* Moraceae/Urticaceae, Combretaceae /Melastomataceae and Myrtaceae) as well as Sapotaceae 1 and Bignoniaceae 2. The highest peak of *Aldina* throughout the core is comprised between zones 2-B and 2-C, and in 2-C ferns like *Asplenium/Blechnum* and *Polypodium* 1 are abundant while fungal remains are not.

3.4.3. *Zone 3 (200-82 cm).* Along this period algae are low, ferns are comparatively moderate and fungal remains reach their maximum representation. Given the suppressing trees percentage, herbs are noticeable as well as montane elements. *Ouratea* is a feature of the zone with an initial peak, but among the most abundant types no remarkable variation is clear. Indeed, a perception of this zone would be a high number of rare elements appearing and disappearing, which would then cause a marked turnover. Among an average of ~150,000 grains/g in zone 3, a high pollen concentration (380,000 grains/g) is seen at 175 cm and very low ones at126 and 136 cm, 76,000 and 41,000 grains/g respectively. Sedimentation rate between 113 and 160 cm is 0.021 cm year^{-1}. In subzone 3-B, algae and fungi are decreasing while ferns increasing, sedimentation is lower, 0.002 cm year^{-1}, that is when black gyttja ends and a new stratigraphic unity appears.

3.4.4. *Zone 4 (82-58 cm)*. This zone corresponds to the full-late glacial period (35-12 Ky BP), sediments are oxidized, nodular clays. The first portion of the zone (4-

A) has more algae, fungal remains, and less ferns, *Podocarpus* reaches its highest representation (5%). *Mauritia* and *Mauritiella* are present before shrinking to zero in 4-B, where ferns reach their highest peak. *Ilex* and *Hedysomum* have their highest percentages, Poaceae is only 3,6%. One single grain of *Alnus* was found. Zone 4 is the lowest concentrations of the core, averaging around 48,000 grains/g and reaching 37,000 grains/g at 69-71cm. At this sample, no algae cyst and fungal hyphae were found, but only 6 fungal spores. A portion of 27% of the grains could not be identified, many of which were broken and smashed, likewise many of the spores that given the very low total pollen concentration, have a remarkably high concentration here. This zone also includes a small distinct layer between 60 and 63 cm (not shown in the lithology of the pollen diagram) that is somewhat grayish. Sediment were deposited at a very slow rate, about 0,0017 (4-A) and 0,0026 (4-B) cm year^{-1}, but an even slower rate is found between 82-84 cm (0.00028 cm year^{-1}).

3.4.5. *Zone 5 (58-0 cm)*….rever sequencia…. The Holocene is more evident for high abundances of palm pollen combined with *Sagittaria,* not to mention all pollen *taxa* cited in Zone 1. Total pollen concentration is very high (average of ~385,000 grains/g), reaching ~653,000 grains/g at 20 cm. The first sample analysed (9-11 cm) had one single grain of *Podocarpus* and the third (29-31 cm) two of *Hedysomum*. During the early Holocene, total pollen concentration is lower, 130,000 grains/g. Subzone 5-A has a markedly high peak (64%) of *Mauritia* and at this same sample total ferns are still high, tapering upwards. The upper Holocene has the lowest ferns counts of the entire profile. Sediments in zone 5 are soft black gyttja, that accumulated at different rates of approximately 0.001 (5-A) and 0.012 (5-B) cm year^{-1}.

3.5. Concentration of palynomorphs x Sedimentation

The pollen histories of lakes Pata, Verde and Dragão (Bush *et al*, 2004) revealed a complex pattern of pollen accumulation in sediments. Nodular clays and more soft gyttjas did not follow one only trend in pollen concentration, but reverse ones. Simple predictions could be of (*i*) higher pollen concentrations in more carbonous sediments, like black gyttjas, and, to the contrary, (*ii*) lower concentrations in less carbonous sediments, like noludar ones that may have evidence of oxidation. Nevertheless, the general assumption of Bush *et al* (2004) is that where sedimentation is slower, more pollen grains will concentrate and, contrarily, where sedimentation is fast, less pollen will. For instance, the nodular clay unity in Pata's lithology (63-83 cm) had very high pollen concentrations (600,000 and 800,000 grains cm^{-3}) and is explained as (quoted literally) "…Such high concentrations were consistent with a very slow accumulation rate, and suggest that the sediments were not dry enough to be fully oxidized'', hence neither (*i*) nor (*ii*), but (*iii*).

Analyzing all three diagrams we see important differences regarding total concentration (TC). Dragão diagram shows low TC at the yellowish nodular gyttja unity (*ii*), the peak of concentration at a khaki nodular gyttja unity (*iii*) and still high concentration at a green-gray gyttja unity (*i*). The low TCs during mid-Holocene are explained by more profund drying with oxidation playing a role. Spores concentration follows the same overall pattern, low and high concentrations concomitants to the TC. Pata shows high TCs at the black gyttja unities (*i*) but extremely higher peaks at the yellowish nodular gyttja (*iii*). At 60 cm, a percentage peak of more than 60% of the spore *Blechnum* is completely absent in its concentration diagram, this is strange because once being shown separately one would expect to see a correspondent concentration diagram according to the percentage one. Verde has high TCs at black and green-gray gyttjas (*i*) and also low TC at green-gray gyttjas (*ii*). Like Dragão, and unlike Pata, spores concentration in Verde is high when TC is high.

The conclusion that can be reached from all three concentration diagrams is that high TCs track slow sedimentation rates, but predicting concentration from lithology is not accurate. This is best evidenced by seeing that the nodular yellow clays in Pata and Dragão have, respectively, high and low total concentrations. Likewise, the khaki nodular gyttja unities in Dragão and Verde have, respectively, high and low concentrations.

The contrasting concentration values of nodular clays during the late glacial (22-12 Ky BP) in Pata and Dragão, no sediment accumulation during the full glacial (35-22 Ky BP) in Dragão, very slowly in Pata with nodular clays, and coarsely laminated sediments in Verde, not to mention the evidence for millennial hiatuses, give rise to an interpretation at local scale of all lakes having dried up either occasionally or for millennial periods.

Our concentration data (Fig.6) strikingly contrasts with previous values at Pata. Assumptions of low pollen concentration in less organic rich sediments (*i*) and the contrary (*ii*) are readily recognized. During the full-late glacial and early Holocene, concentrations are lower, in contrast to the upper Holocene and last interglacial. We therefore suggest oxidation played an important role in diminishing pollen quantity, which very well fits the argument of accumulation of clastic material by remobilisation (Santos *et al*, 2001; Barbosa *et al*, 2004). A support for this is the high amount of spores when concentration reaches its minimum. Spores tend to be more abundant when humid conditions favour them to grow near depositional sites, or when sediment reworking selectively preserved more spores due to their better resistance (Colinvaux *et al*, 1999), the latter is obviously the case.

All these conclusions are notwithstanding supported by data from Carajás (Absy *et al*, 1991). The more organic rich is the sediment, the more abundant forest elements are represented, and higher is pollen concentration. To the contrary, when clastic material is accumulated, pollen concentration drops sharply (Absy *et al*, 1991 and Absy, unpublished data). Other pollen sites where concentration data are available provide important similarities, like in SW Amazonia (Noel Kampf), the low concentration of pollen is explained by low sedimentation rates that caused superficial sediments to be oxidized (Burbridge et al 2004). Likewise, in Central Brazil (Vereda das Águas Emendadas; Barbieri *et al*, 2000), the drastic decrease in palynomorphs concentration is interpreted as drier and more seasonal climatic conditions, also during the LGM and early Holocene.

4. Discussion

4.1. Inferring the vegetational type from the fossil record

4.1.1. Interpretation of the zones. A "climatic optimum" similar to those of upper Holocene is probable to have existed in Zone 1, for all characteristics mentioned. The nature of the sediment, the palynomorphs concentration and the pollen assemblage leads to the interpretation that the high occurrence of *Pteris/Pitirograma* indicates superhumid conditions rather than any depositional feature related to selective preservation. Such palynologycal data suggest this zone comprises the last interglacial period, that has its lower boundary at about 110 Ky BP. However, it is not possible to establish precise boundaries in this zone as our analyses end up abruptly on its onset. From zone 2 to 4 the inferred climatic configuration suggests a slightly drier and cold condition, seen from lowered lake level and cool adapted taxa. Such conditions are stronger in Zone 4, where the lithological characteristics coupled with palynologycal data indicate a drying of the lake. Finally, the Holocene shows two distinct phases (5-A and 5-B), with a superhumid condition like present having been reached around 6 Ky BP, before that the climate was probably still more seasonal and lake level lower. Zone 5 is the correspondent Pata 4 zone in Bush *et al* (2004), where it is mentioned that, “An unknown pollen type, a small tricolporate reticulate grain occurred as a rare component in many samples, but reached a peak occurrence of 55% in a single mid- Holocene sample”. This is very much surprising since no pollen percentage scale even reaches 50%, and once small tricolporate grains were included in the ‘other arboreal’ sum (their ‘rule of thumb’), it would be presumably expected to see the ‘other arboreal’ reaching this 55% at such sample, but it did not. Possibly this pollen type was somehow omitted, or an analytical problem caused this outcome.

In general, pollen zones become rather artificial if one thinks of vegetation, but not if limnological conditions are taken into account. We suggest that higher total concentration and algae percentage are evidences for enhanced lake eutrophism, like for instance during interglacial times.

Major biome changes are easy to be identified in a pollen record, like the replacement of forest by savannah. The nearly constancy of pollen assemblage through Pata’s history can be interpreted as unbroken forest with elements that are presently confined, though not necessarily (Van Der Hammen & Hooghiemstra, 2000), to montane areas, and this has been shown to compose a nonanalog vegetation (Behling, 2001; Colinvaux *et al*, 2001a, Ledru *et al*., 2001, Burbridge *et al.*, 2004), being a modest cooling the factor governing plant communities reassortment. While this hypothesis becomes a strong ecological statement, if not yet, it is still questionable whether a cooler and wet, or cooler and dry climate prevailed. In adittion to this, the extent to which plant communities reassorted can be tested.

The best way to calibrate paleopalynological interpretations is to analyse them under the light of present day pollen spectra. Up to date, the most informative and distinctive pollen rain data for the neotropical lowland region is provided in Gosling *et al* (2009), who comparatively studied different vegetational formations in southwestern Amazonia. The strongest differentiation possible to be made is assigning Moraceae/Urticaceae (>40%), *Cecropia* (>3%), *Hyeronima* and *Celtis* as indicative of moist evergreen tropical forests. While *Hyeronima* and *Celtis* are rare elements in our records, not suitable for such a discussion, Moraceae/Urticaceae and *Cecropia* are found in both pollen rain samples and sediments. All six pollen rain samples (five in Bush *et al*, 2004, and one here) are very similar regarding the abundance of these two *taxa*, Moraceae/Urticaceae never exceeds 15% (generally less) and *Cecropia* is rare, we found only two grains (<1%) and Bush *et al* (2004) certainly less than 2% in only one sample. To the extent comparisons can be drawn (given the non systematic nature of both pollen rain studies), the two records indicate a moderate lower representation of evergreen forest during the middle to late glacial, probably due to mesic conditions at the hill instead of complete tall forest cover. On the one hand, we reckon a methodological problem might have decreased the quantities of very small grains (Salgado-Laboriau, 2007) like *Cecropia* and some Moraceae/Urticaceae, which we do not believe bias our interpretation; but on the other, it is noticeable that our Moraceae/Urticaceae abundances are more similar to the pollen rain spectra and hence may not be biased. Anyway, the lower abundance of such grains allowed other types to be better represented, and this was crucial for recognizing the local paleovegetation.

In woodland savannah and seasonally dry tropical forest (SDTF), the presence of spores is more indicative of these vegetation types than it is for evergreen forests. The upper Holocene sediments of lake Pata contained few spores, and during the full-late glacial they have higher richness of types and relative abundance. This may be another argument in favour of a more seasonally dry vegetation. Bush *et al* (2004) interpreted spores abundance as a signal typical from evergreen moist forests, we do not, however, believe so, because when one compares glacial time sediments to Holocene ones, the difference in both richness and abundance is high. Given that no other period has moisture levels as high as the Holocene (apart from the last interglacial), an important argument raises for assigning spores to a community change. It is also true that not only SDTF show higher abundances of spores, but also montane communities when compared to near lowland ones (Weng *et al*, 2004).What is more, the presence of montane elements does not preclude the existence of a SDTFs, for instance Rodgers & Horn (1996) found montane elements like *Weinmannia* in a pollen rain study performed at a SDTF.

With regard to Poaceae pollen, some evidences indicate the possibility of open vegetation like the woodland savannah not being dominated by Poaceae in the fossil records (Ledru, 2002; Golsing *et al*, 2009). Indeed, even a gradation was found by Ledru (2002), showing more grass represented in the pollen rain samples according to the degree of openness of the cerrado formation, thus exhibiting an expectable relation of the degree of canopy openness with grass pollen representation, and hence providing an important argument as a more sensitive proxy. Nevertheless, using Poaceae pollen as sensitive indicators in forested areas is rather problematic, it may become a good indicator of precipitation and seasonality change when rainfall falls below 2,000 mm (Bush, 2002). Present day precipitation at the Hill of Six Lakes is around 3,000 mm, if the predictions of Van Der Hammen & Hooghiemstra (2000) are correct, precipitation may have reached some 1,500 mm, in events when the lake dried up. In this case we may be on the edge of Poaceae pollen becoming an indicator, and in spite of still being a poor tool for reconstructing the local paleoenvironment, the moderate increase in Poaceae and other herbs may signal some openness during mid to late glacial (seen in pollen zones 3 to 4, likewise montane elements).

When comparing pollen rain data with fossil assemblages of Lagunas Bella Vista and Chaplin (Burbridge *et al*, 2004), Gosling *et al* (2009) point out evidences of dry forest during the last glacial being represented by *Machaerium* type, *Paullinia/Roupala* and Myrtaceae, and others, which are also found in Pata’s record. The decrease of these *taxa*, coupled with the increase in Moraceae/Urticaceae abundance would mark the beginning of present day climate and forest structure. This trend is also seen in the Lake Pata record, in a more moderate level. Indeed, not only Myrtaceae but also Combretaceae/ Melastomataceae and *Pouteria* (majority within Sapotaceae 1) can be components of SDTF and woody savannah’s pollen rain spectra, respectively, and the same trend above cited being found for Combretaceae/Melastomataceae and *Pouteria* may indicate, again, the presence of dry forest at the hill during the last glacial. Other *taxa* that are often cited as important components of SDTF are legumes and Bignoniaceae (Pegnnington *et al*, 2000), the present record shows very clearly the higher percentages of Fabaceae prior to Holocene. Bignoniaceae is likewise similarly well represented. Some *taxa* within Fabaceae are especially important as indicators of drier forests, like *Bowdichia*, though not quantifiable (see results 3.3). Apocynaceae and Rubiaceae may show the same indications.

4.1.2. *What was the vegetation really like?*

After the publication of the first pollen diagram from the Hill of Six Lakes (Colinvaux *et al*, 1996), Pennington *et al* (2000) raised the possibility of a broad expansion of SDTF based on the similarities at generic level of the fossil assemblage at Pata with SDTFs. Bush *et al* (2004) refuted this hypotheses based on the distinctive Poaceae pollen representation in savannahs' pollen rain studies and on the lack of high quantities of charcoal. Moreover, a pattern of no *taxon* being overrepresented and a general high arboreal diversity would be crucial for viewing the paleovegetation at the hill as clear signal of uninterrupted forest cover, what is interpreted as long-term lowland biome at the regional scale, with only cooling playing a role in reassorting the vegetation.

However, for all reasons discussed above (4.1) we claim there is room for the interpretation that during the last glacial period the vegetation at very local scale had a structure similar to those found nowadays in dry forests. It is obvious that using the blend of most abundant *taxa* for such interpretation can be misleading, since they belong to different vegetation types. So a good comparison would be seeing how the same controversial *taxa* behave in other pollen site in Amazonia, where the vegetational change is clearer. Carajás share some of the most abundant *taxa* with Pata, *Aparisthmium*, Melastomataceae and Moraceae have the general same trend of abundances: *Alchornea* is an abundant element of the upper Holocene and low represented during the glacial period, Moraceae shows the same pattern, and Melastomataceae the contrary, being more representative during the glacial (Absy *et al*, 1991 and Absy, unpublished data). The strongest difference is openness evident from herbaceous pollen. At Maicuru (Colinvaux *et al*, 2001b), where a clear sedimentary gap of almost 15 Ky exists during the full-late glacial, similarities are found for

Alchornea/Aparisthmium, *Cecropia*, Melastomataceae, Myrtaceae and Moraceae/Urtiaceae.

The best indicator proving the existence of non-analog vegetation during most of the last glacial period, at least at the very local scale, is *Aldina*. Its present altitudinal range never exceeds submontane biomes, and its representation in the fossil record is nearly constant throughout the core (Fig. 5 and 6). This, coupled with the invasion of montane elements, suggests the level of NAV's reassortment as a moderate one.

Aldina is widespread in the Rio Negro basin, often cited in the RADAMBRASIL (1976) inventories. In Central Amazonia, *A. latifolia* is very common and dominant in black-water flooded forests (Parolin *et al*, 2004). In relation to scleromorfism, which is characteristic of all campinas types, populations of *A. heterophylla* studied near Manaus showed similar degrees of leaf scleromorfism when comparing different habitats of Amazon caatingas (open, tall and shaded), but showed better environmental adaptation for tall campinas (Araújo & Mendonça, 1998). At the same site Roberts *et al* (1999) showed that leaf flush pattern is linked to the start of the dry season, defined by the first month where potential evapotranspiration exceeds precipitation. Individuals of *Aldina* collected in the Pico da Neblina National Park, near the Hill of Six Lakes, have dry, large-seeded sclerocarpic fruits comparable to those of the Guaiana Shield legumes (Boubli, 2002). It is clear that *Aldina* commonness is related to its ecological successfulness and plasticity, inferred mainly from the fact that it tends to be more abundant in habitats where water stress has an influence in the physiognomy (e.g. flooded forests and heath forests of Hydromorphic Spodosols). We then hypothesize *Aldina* was able to resist slight climatic changes within the hill by means of displaying phenotypic plasticity, to a extent sufficiently resistant to cooling, or the other way round, temperature depression was not high enough to destabilize *Aldina* population, whereas climatic changes may have affected more other *taxa*.

Unquestionably, the hill underwent a cooling during the last ice age, more evidently at the glaciation peaks. The most important paleobotanical record is the occurrence of *Podocarpus, Hedyosmum* and *Weinmania,* which is consistent with a temperature depression in the order of 4-5%. For its higher abundances, *Podocarpus* is a key *taxon.* Bush *et al* (2004) stated that three phorms of *Podocarpus* pollen were found, two of which differ mainly in size, and the photomicrographs show these three phorms but has no scale bar. The two most common *Podocarpus* species in Brazil (*P. sellowii* and *P. lamberti*) have been studied by Barth (1962) and the author concluded it impossible to distinguish between the two species using their sizes. In addition, *Podocarpus* found in the pollen spectrum of bees in Manaus showed a great variation in pollen shape and size (Marques-Souza, *in press*). Unlike Bush *et al* (2004), we do not believe three species invaded the hill, this would be underestimating variation in pollen morphology.

4.2. Other regional evidences

Some independent sources from geological studies provide evidences for a drier climate in north Amazon. Upstream the Rio Negro course, clear relict eolian dunes strengthen the argument claiming for drier periods during Peistocene-Holocene in the region (Carneiro-Filho *et al*, 2002). In the Roraima-Guayana region, again relict eolian dunes were found and suggest a late Pleistocene dry period, with wind direction the same as that of the modern annual dry season (Latrubesse & Nelson 2001). In such cases, because dune activity suggests a very sparse vegetation cover, the late glacial scenario is even more drastic than those predicted from pollen sites, especially Pata.

Eolian activities are elsewhere seen in central Amazonia (Iriondo & Latrubesse, 1994). With respect to the Negro Basin, it is interesting to notice that the mid glacial alluvial deposits carried abundant quartz sand, which can be accounted as a product of more seasonal conditions in the upper chachment (Latrubesse & Franzinelli 2005). Dry late glacial conditions are as well evident from different landforms, where aridity affected steam activity and semi-arid forms occurred at the LGM (Thomas & Thorp, 1995).

The regional morphoclimatic evolution, as discussed in RADAMBRASIL (1976), reveals a generalized past dry climate. The pleistocenic pediplanation which took place in the Rio Branco-Rio Negro region created several small residual inselberg-type reliefs that have just recently been colonized by vegetation covers. Furthermore, at some sites within the Pediplain, incompletely consolidated ferrugineus concretions very clearly indicate that there was an interval of climate with dry and humid season during the elaboration of the Pediplain. Although such structures can date some million years (as argued by Colinvaux & de Oliveira, 2001), many stone lines in the Amazon are Pleistocene aged and have present day analogues in savannah patches within the Amazon (Costa, 1991).

4.3. Lake level and seasonality

Variation in lake level was explained as a cause of orbital forcing (Bush *et al*, 2002). Precessional cycles would have reduced the precipitation during the wet season (December-January-February, DJF), and therefore the long episodes of lake lowstand would enhance productivity of planktonic and benthic algae. These phases of lake eutrophism are suggested to have concentrated K^+ within the system which was inferred from the paleochemical record. All this interpretation is based on the cyclic nature of K^+ peaks and algal blooms coinciding with these peaks at the nodular sediments, but only one peak is comprised within the range of C^{14} dates, around 15 Ky BP, when sedimentation is very slow. Moreover, some estimates of algal remains concentrations are given, but not systematically like it is here. Although it may be questionable that counting algal cysts is somewhat biased by cysts fragmentation, samples prepared equally and counted by the same analyst are fairly comparable among them.

Our quantitative data contrasts with the previous interpretation because samples at the nodular clay unity presented comparatively low concentrations of algal cysts (Fig. 6). Indeed, between 69 and 71 cm, which dates back to the LGM, no algal cyst was recorded. Hence, during the LGM the lake may have dried up for longer than episodically. The low algae concentration extends up to the early Holocene, and is very high at the upper Holocene as well as at the last interglacial. We cannot strongly refute the intricate lake level dynamics because our subsampling interval is less refined than the previous analyses, but our data firmly suggests that eutrophism, and hence algae concentration, has a relationship with humid periods, that is, if sedimentation was always constant. However, the erosional event proposed by Santos *et al* (2001) agrees more with our data suggesting a drier and more seasonal LGM. Actually, if sedimentation was never interrupted we have a clue for a slightly humid interval during the late glacial- LGM, when algae and fungal remains increase while total spores, which may then be related to sediment remobilisation (through selective preservation), decrease (pollen sub-zone 4B).

Because it is seasonality and not total precipitation that sets biomes where rainfall is >2000 mm (Sternberg, 2001; Bush *et al,* 2004b) and no significant change in pollen assemblage was found, Bush *et al* (2004) interpreted there was no decreased precipitation during June-July-August (JJA). It is quite reasonable to expect precipitation reached at least 2000 mm during dry phases of the last glacial and even less in events when the lake dried up (Van Der Hammen & Hooghiemstra, 2000). In addition, local convective activity is the responsible for most rain events (RADAMBRASIL, 1976), and this continental moist air mass certainly significantly diminished its strength since vegetation cover was not as massive as nowadays during the glacial period, which reflects in lower water supply from the evaporating ground. An orographic source of moisture cannot be discounted, and neither can the effect lowered temperatures cause in evaporation, especially uphill. All this, coupled with the evidences of torrential rains that caused erosion, pollen data indicative of some moderate community reassortment resembling dry forests, low lakestands more plausibly occurring during enhanced “dry” seasons, not to mention evidences from other sources of data suggest an overall scenario far from untouched forest cover. Based on the combination of several data sets, we propose the regional climate was seasonally drier during the last glacial cycle, especially at the full glacial period.

4.4. Climatic evolution

By constraining the basal age of the core in 120,000 BP, the major climatic events of the last glacial period become consistently reflected in the lake system (Fig.7). Phases of lake eutrophism, when algae and pollen concentration are higher, coincide with “climatic optimums”, these are MIS 5e, 5a, onset of MIS 3 and MIS 1. On the contrary, phases of ice sheet enhancement generally coincide with lake lowstand, and poorer preservation, MIS 5e, offset of MIS 5, MIS 4, MIS 2 and onset of MIS 1. The important role that selective preservation plays is readily seen when one realizes pollen concentration is somewhat in contrast with spores percentages, especially in strong sedimentary events like the LGM. With total absence of algae cysts, spores peak, and, interestingly, with a slight increase in pollen and algae concentrations, spores fall in the onset of MIS 2 (pollen sub-zone 4-A).

Changes in lithology also reflect climatic phases. The only contrasting point is MIS 5e and MIS 4, when dark brown silty clays seem to follow different environmental conditions, however the formation of such sediments is unclear and our biotic proxies are consistent with major global climatic events. Changes in the biotic proxies not reflected in the lithological unities may be due to more complex bioclimatic settings not prone to analogies with isotopic stages. For instance, the hypothesis of Bush *et al* (2002) of K^+ peaks owing to lake lowstand and thus enhanced eutrophism, is not mutually exclusive from oxidation playing a major role in establishing palynomorphs' concentrations. If short phases of enhanced eutrophism caused by lake lowstand did incorporate K^+ in the sediments, poorer preservation in the intervening troughs diminished concentrations, being the later a grosser proxy than the first, but more reliable since absolute counting is less likely to errors. Finally, how to explain sediments without algae remains if not by oxidation? Furthermore, dating the basal age of the core by means of using the cyclic nature of K^+ stands in sharp contrast to our suggesting of dating around 300 cm to the last interglacial, which we think is pretty more consistent based on the indicative pollen assemblage. If their extrapolation is correct, it would mean that the same sedimentation rate occurred at different lithological unities, which is senseless.

A well balanced paleoenvironmental conditions modeling by Cook & Vizy (2006), which includes the meaningful topographic variable into the analysis, showed the reason why seasonality was enhanced in the Amazon basin during the LGM was a delayed start of the moonson annual period. This is in agreement with Santos *et al* (2001), Barbosa *et al* (2004) and the present interpretation. Their simulation reveals a

25-35% lower annual rainfall, which very well fits measurements of Van Der Hammen & Hooghiemstra (2000) as well as a threshold of seasonality playing a more important role than total annual precipitation in setting biomes. In their model, Cook & Vizy (2006) point out two extra Amazonian regions of particular interest, the Andes and the semi-arid Brazilian Northeast, both of which experienced wetter conditions at the LGM. Independent field work prove this true, in a remote semi-arid site in NE Brazil data from speleothems and travertines demonstrate that wet events have occurred during much of the Pleistocene, allowing the formation of a semi-deciduous forest linking the Amazon basin to the Atlantic rain forest (Auler *et al*, 2004). The Andean region is more complex, with wetter and drier periods co-occurring, for instance the Bolivian Altiplano that underwent wetter (Chepstow *et al*, 2005) and drier (Argollo & Mourguiart, 2000) conditions at the LGM.

In relation to cooling, polar air advections may have been the source of lowered temperatures (Latrubesse & Ramonell, 1994), this is correspondent to the present day “friagem” events in south-southwestern Amazon taking place during the dry season. This seasonal approach regarding glacial cooling combined with warmer annual periods caused by the disabled latent heat flux from the surface (Cook & Vizy, 2006) suggests higher temperature amplitude and instability. The overall temperature depression suggested on the order of 4-5°C is in contrast to Cook & Vizy (2006), whose model predicts a cooling of more or less 2°C, which is in agreement with sea surface temperature decreases at the LGM. The clue of montane elements being found in the pollen rain spectra at the hill (i.e. *Myrsine*), *Podocarpus* and *Hedyosmum* found in upper Holocene sediments (also seen in the previous diagram for *Hedyosmum*), the contrasting picture of a forested hill against a more drastic dry scenario in the lowlands, coupled with Cook & Vizy's (2006) modeling may suggest that a 4-5°C temperature depression is exaggerated.

The strongest signal in the record is the erosinal event that occurred at the LGM. Santos *et al* (2001) and Barbosa *et al* (2004) interpreted this event as a cause of a markedly increased seasonality, with torrential rains and cooler temperatures, typical of seasonal climates. This fits very well our interpretations. What remains unresolved is whether the rest of the glacial followed the same trend or not. A simplest view would agree with one only pattern setting the climate, and hence most of the glacial would be a less expressive climatic expansion of seasonality to the north, like it is nowadays in central Brazilian biomes. No other clue proves the contrary, thus it seems reasonable to accept seasonality as the feature governing the bioclimatic regional evolution throughout the last glacial.

5. Concluding remarks

The pollen record from Lake Pata has been interpreted as a continuous register of lowland forest in northwestern Amazonia. The discrepancies in the chronostratigraphies of different cores plus at least two clear problems with the pollen diagram of Pata (an omitted grain and the strange low concentration of high percentages of spores) raised the possibility of a reanalysis being plausible. Our new pollen analyses and interpretations, compiled with some other scattered regional evidences show that the Six Lakes Hill must have been a site with slightly altered forest in a more arid region (which has nothing to do with the refuges hypothesis) and not the contrary as proposed by Colinvaux (1998). The main source of change is seasonality, seen from both rain season delay (Cook & Vizy, 2006) and annual polar cold air masses advection (Latrubesse & Ramonell, 1994). The contrasting points emerging from paleobotany and geology cannot be resolved as mutually exclusive ones. Rather, they should compose a more complex environmental situation, seen at the hill as the result of an altitudinal moisture distribution unparalleled to the lowlands.

The extent to which the forest was affected by climatic changes is a little obscure. Whereas it is clear that during MIS 2 a strong event occurred, it remains to be explained what the landscapes were like during phases not as dry as MIS 2 and not super humid like the present and past interglacials.

Acknowledgements

We would like to express our sincere thankfulness to Antonio Rossi, who kindly provided the sediment samples. This work was supported by CNPq. All administrative duties were facilitated by the Botany Department at INPA.

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Conclusão

O registro polínico dos sedimentos da lagoa da Pata tem sido interpretado como um contínuo de floresta na região onde é situada. Diferenças nas cronologias estratigráficas de núcleos de sondagens distintos, mais pelo menos dois problemas bem evidentes com o diagrama polínico da lagoa da Pata, que são a omissão de um grão e a baixa concentração de esporos mesmo estes tendo uma alta porcentagem, fizeram com que uma re-análise fosse plausível. Os dados do presente trabalho, bem como as interpretações compiladas com outras evidências regionais mostram que o morro dos seis lagos foi um ponto de floresta levemente modificada em uma região mais seca (o que não pode erroneamente interpretado a luz da hipótese dos refúgios) e não o contrário como proposto por Colinvaux (1998). A maior fonte de mudanças climáticas foi o aumento da sazonalidade, vista pelo atraso na estação chuvosa (Cook e Vizy, 2006) e chegada de massa de ar frio polar (Latrubesse e Ramonell, 1994).

A extensão com a qual a floresta se modificou pelas mudanças climáticas é um pouco obscura. Enquanto um forte evento climático é evidente na MIS 2, ainda está por ser explicada a configuração das paisagens pleistocênicas durantes fases não tão secas quanto a MIS 2 e não tão úmidas quando o presente.

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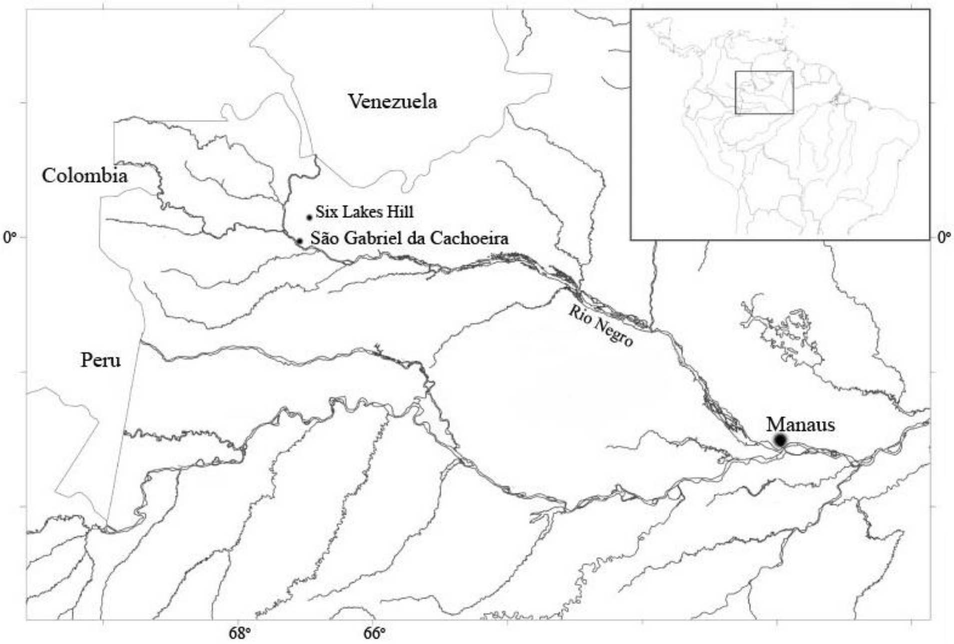

Figure 1: Sketch map, indicating the approximate location of the Six Lakes Hill, in the upper Rio Negro Basin.

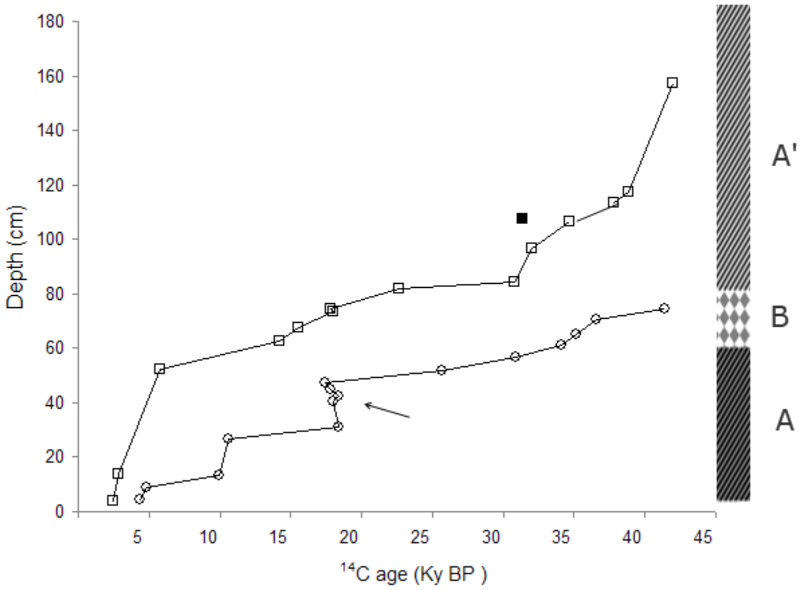

Figure 2: Interpolations of depth and age. Combined principal and parallel core (squares) and the core studied by Santos *et al* (2001) (circles). Note the stratigraphic column is only correspondent to the principal and parallel cores. Arrow (erosional event), shaded symbol (excluded date), soft green-black gyttja (A), yellowish nodular gyttja (B) and bluish black gyttja (A`).

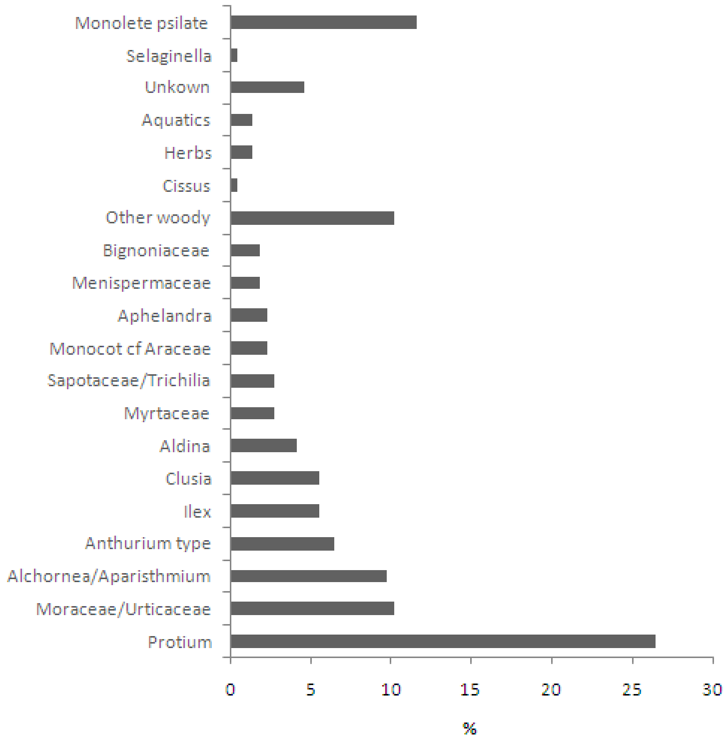

Figure 3: Most abundant *taxa* found in a moss polster sample collected at the Hill of Sixs Lakes (216 pollen counted, spores percentage are calculated on the basis of the pollen sum).

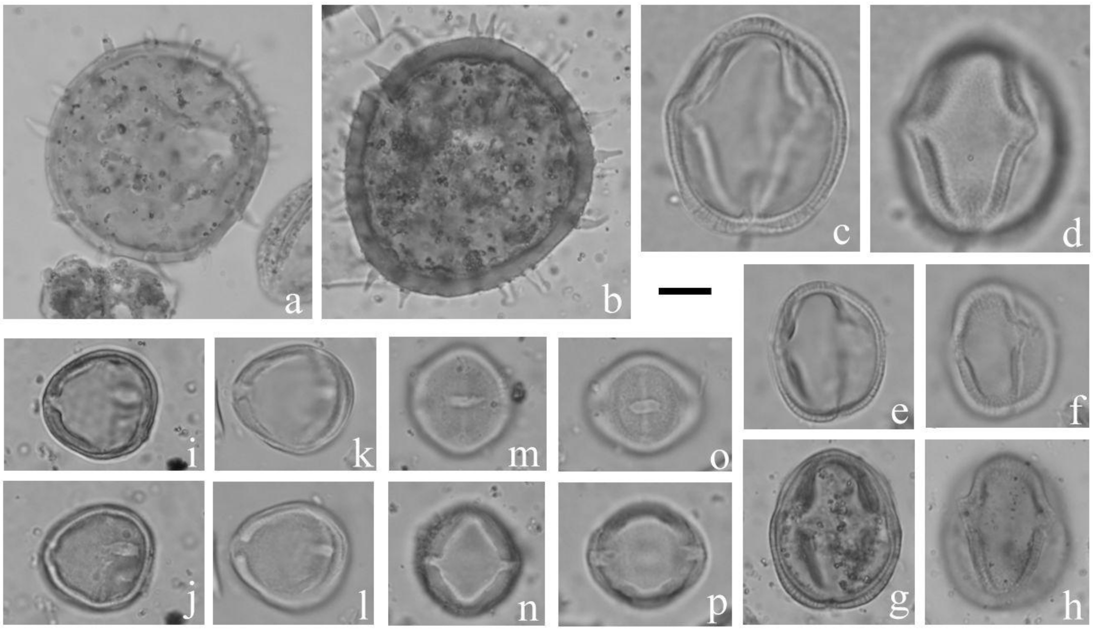

Figure 4: Fossil and recent pollen; (a) fossil *Mauritia,* (b) fossil *Mauritiella*; (c-d) *Aldina latifolia* Spruce ex Benth.; (e-f) *Aldina heterophylla* Spruce ex Benth*;* (g-h) fossil *Aldina;* (k-l and o-p) recent *Ouratea* (collected at the Six Lakes Hill and yet not identified to species level); (i-j and m-n) fossil *Ouratea*. (Scale bar= 10 µm).

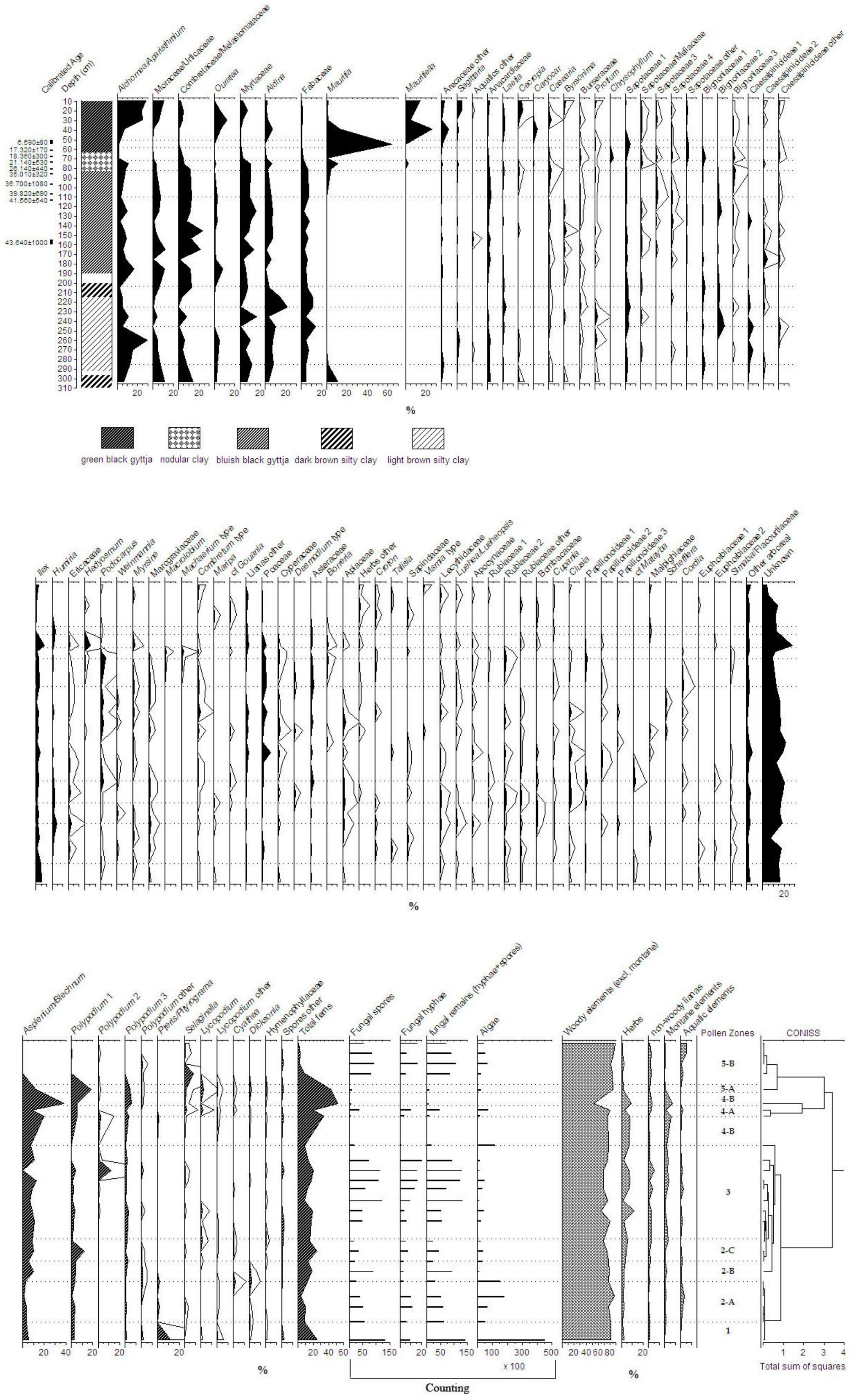

Figure 5. Percentage pollen diagram of Lake Pata.

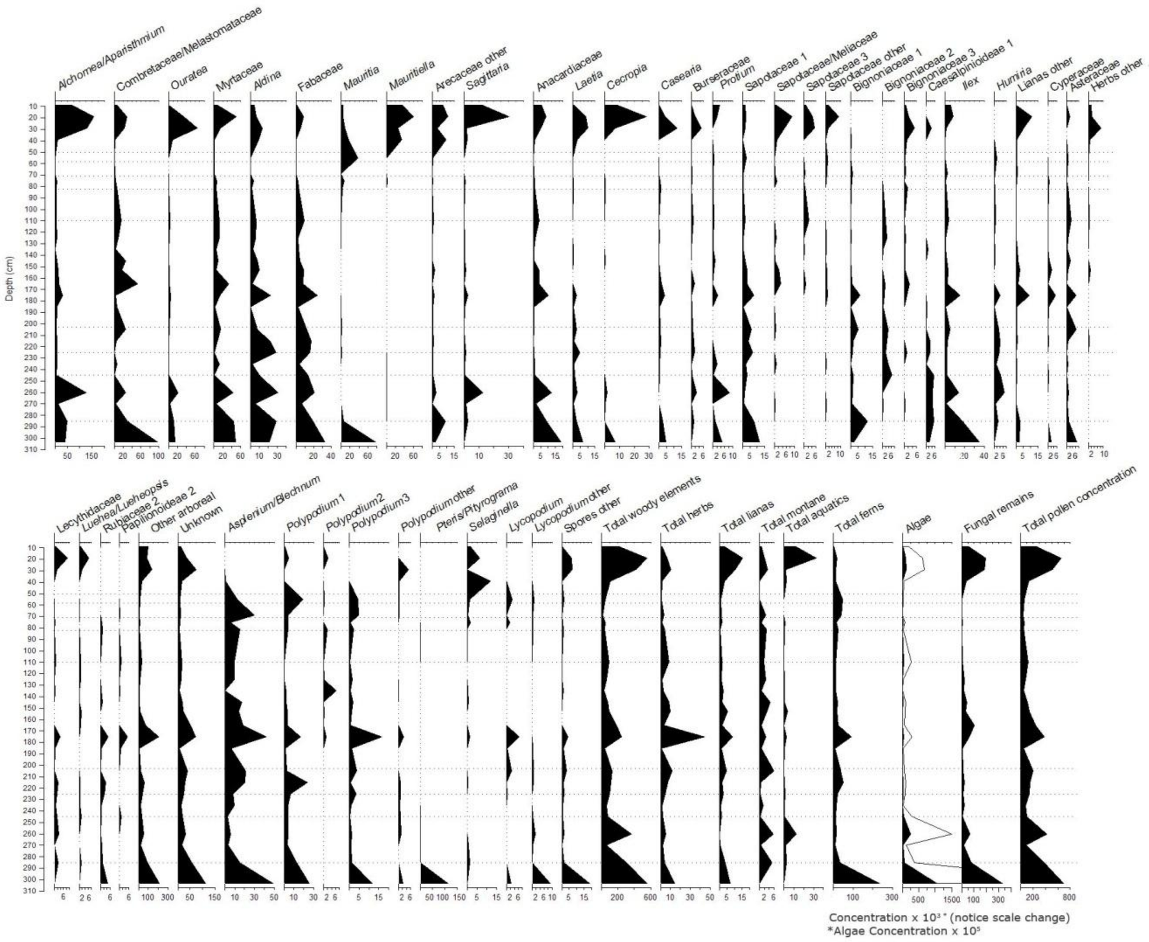

Figure 6: Concentration pollen diagram of Lake Pata.

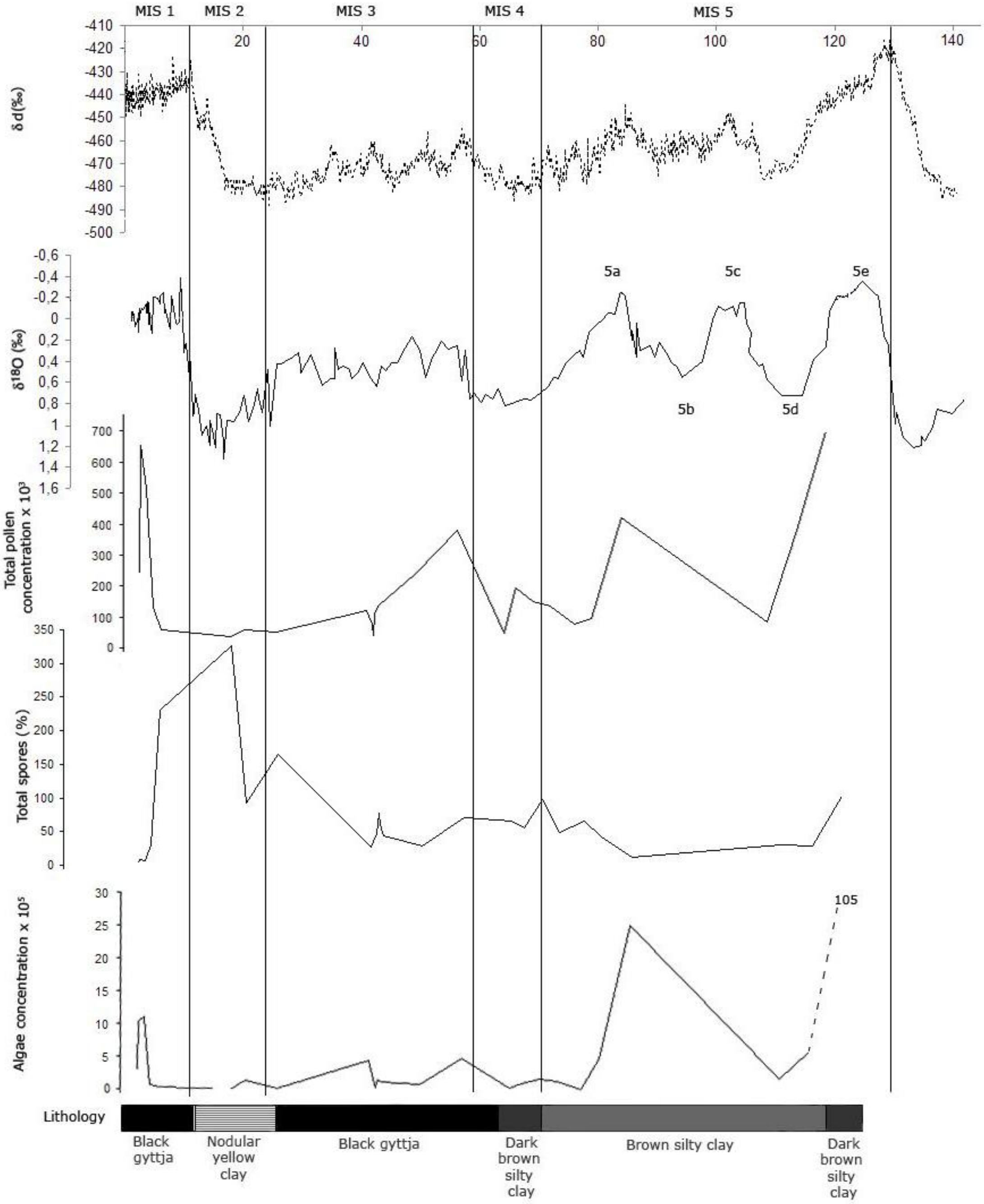

Figure 7: Deuterium and isotope oxygen records from Vostok (after Petit *et al*, 1999), algae and pollen concentrations and spores percentages from sediments of Lake Pata.